

Reproductive ecology of the bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest

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Abstract

The reproductive pattern of the bat *Carollia perspicillata* (Linnaeus 1758) was studied in a forest fragment of the Atlantic rainforest in southeastern Brazil from November 1997 to June 1999. *C. perspicillata* showed a seasonal bimodal polyoestrous pattern, with its highest reproductive peaks during the wetter months and lesser peaks during the drier months. Several other aspects were also affected by rainfall: at the end of the dry and wet seasons, number of juveniles was highest (reflecting reproductive peaks), individuals were heavier (indicating better conditions), and activity peaks were shorter and earlier in the night. The influence of rainfall on reproductive patterns is likely to be indirect, its effects being mediated by the availability of food resources, especially fruits, which is probably the factor that does directly affect the reproduction of this species.

Key words: *Carollia perspicillata*, Chiroptera, reproduction, ecology, seasonal dynamics

Introduction

Most acquired knowledge on reproduction of Neotropical bats has come from long-term, detailed studies in Central America (e. g. BAKER et al. 1979; FLEMING 1988; FLEMING et al. 1973; HANDLEY et al. 1991). However, as latitude has some effects on reproductive seasons, results obtained in Central America should not be readily extrapolated to elsewhere in the Neotropics. Several data on the reproduction of Neotropical species have been obtained by studies focusing on other subjects, like communities (RIBEIRO DE MELLO et al. 1999).

On the basis of their classic work in Central America, FLEMING et al. (1973) were the first to list four basic reproductive patterns for Neotropical bats, which were later discussed by TADDEI (1980), with remarks for Brazilian species: 1. seasonal monestry (family Noctilionidae): single reproductive peak during the year; 2. bimodal seasonal polyoestry (family Phyllostomidae, especially the frugivores): two reproductive peaks during the year; 3. a long reproductive period, with a small period of reproductive inactivity (family Vespertilionidae); 4. reproduction throughout the year (the vampire bats, subfamily Desmodontinae, currently included in the family Phyllostomidae).

The work by MYERS (1977), in Paraguay, suggested that there can still be other patterns to be discovered, as in some vespertilionid bats there can be three short reproductive peaks a year, which would correspond to a trimodal seasonal polyoestry.

Several studies have shown that in Brazil the short tailed fruit bat, *Carollia perspicillata*,

a phyllostomid, shows bimodal seasonal polyoestry (FAZZOLARI-CORRÊA 1995; RIBEIRO DE MELLO and FERNANDEZ 1998; RIBEIRO DE MELLO et al. 1999). This is similar to the pattern *C. perspicillata* shows in Central America (FLEMING 1988) and in French Guyana (CHARLES-DOMINIQUE 1991; COSSON and PASCAL 1994). Usually there is a higher reproductive peak (almost simultaneously for males and females) during the local wet season, followed by a smaller peak in the dry season. As this pattern is related to climatic seasons, they are inverted in the northern and southern hemispheres, causing predictable differences between Central and South America, in addition to more subtle geographic variation.

The present study aimed to contribute towards further enhancing the knowledge on the reproduction of *Carollia perspicillata*, a bat species pointed out by many authors (e.g. FLEMING 1988) as one of the main seed dispersers of pioneer plants, especially understory shrubs, in the Neotropical Region. The Brazilian Atlantic Coastal forest is one of the most endangered ecosystems of the World (FONSECA 1985), which makes it very important to gather more details on its key mutualists. Reproductive condition, age structure, sex ratio, mean mass, and activity cycle were studied in a population of *C. perspicillata*, in order to characterize the variation in these parameters through time and to relate them to climatic patterns, particularly rainfall.

Material and methods

Study area

The study was carried out in a forest fragment (area 15 ha) of the Atlantic coastal rainforest within Poço das Antas Biological Reserve (22°30'–22°33' S/42°15'–42°19' W). The fragment is close (<2 km) and thus within flight distance for *C. perspicillata* from the main forest block of the reserve (ca. 3000 ha). The climate of the area is warm and damp; between 1987 and 1998 the mean air temperature was 24.6°C and the mean annual rainfall was 2,121 mm (Programa Mata Atlântica, unpubl. data).

There is a moderate seasonality in rainfall (Fig. 1). The driest months occur between June and August ("dry" season), and the wettest from September to May ("wet" season). The seasonality of rainfall during the last 10 years is shown in figure 1. There is some yearly variation in the exact duration of the seasons. Therefore we used another criterion to characterize months according to rainfall, especially when analysing hourly activity of the bats (expressed by number of captures). We considered the drier months in 1998 to be May–July, and in 1999 to be May–June, because their rainfall indices were clearly lower than in the remainder of the year (see Fig. 2). This seems to be more consistent with the seasonality of fruit production.

The fragment studied ("H") belongs to a system of eight small forest fragments, and its area is the largest among them. The history of the area has not yet been totally revealed, but there is some evidence that it was a natural island system, becoming drier after the building of a dam in the São João River, which drastically altered the water level. Along the edges of the fragment, as well as in its interior, there are many plant species which have been reported in previous studies as being visited by *C. perspicillata*, such as *Piper* spp. (the most abundant shrub in the edge of the fragment), *Solanum* spp. (very common), *Cecropia* sp. (common in the open area-matrix), and *Passiflora* sp. (present in low abundance) (BREDT 1996; CHARLES-DOMINIQUE 1991, FLEMING 1988; SAZIMA and SAZIMA 1978).

Compared to the others fragment H has relatively high trees, which support even primate populations of *Leontopithecus rosalia*, *Cebus apella*, and *Alouatta fusca*. It has a dense understory near the edges, closed canopy (with some gaps) and is connected to a forest "corridor" that leads to the continuous forest. The edges of the fragment are covered by pioneer shrubs (mainly *Piper* spp. and *Solanum* spp.), bracken (*Pteridium* spp.), grass and pioneer trees (like *Cecropia* sp. and *Trema micrantha*), in order of abundance.

Capture and recording

From November 1997 to June 1999, monthly capture-mark-recapture sessions were carried out. Although marking is not useful for the abundance estimation of bats outside large roosts, due to the

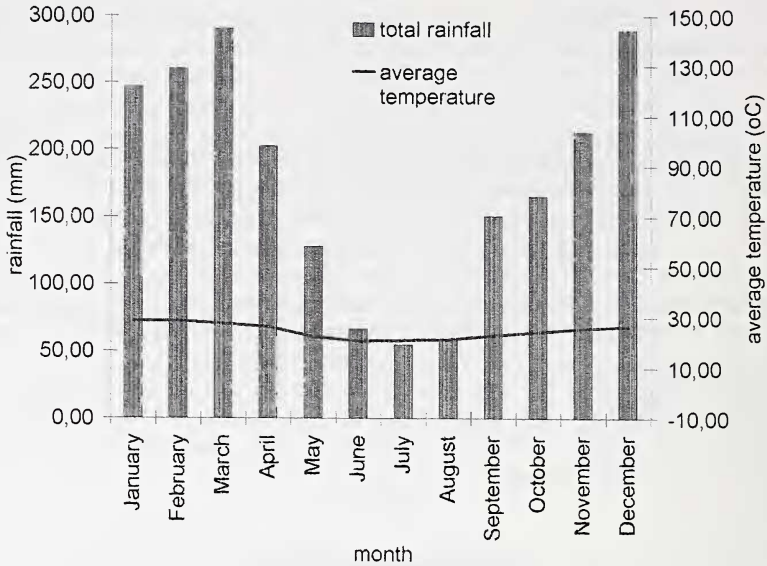


Fig. 1. Variations in rainfall and air temperature for the Poço das Antas Biological Reserve, southeastern Brazil, using the averages for each month for the period 1987–1998.

typical low recapture rates in open areas (KUNZ 1982; KUNZ 1988; FLEMING 1988; SEBER 1982), knowing the number of individuals in the total of captures is important in the procedures of non-parametrical statistical tests.

After being examined each bat was individually marked on the forearm with an aluminium-numbered band (provided by A. C. HUGHES, Inc.). We used aluminium bands to prevent removal by bats, an usual problem of plastic bands. Marked bats had some eventual injuries, but these could be reduced by using bands larger than the circumference of the forearm. The code contained the letters UFRJ (Universidade Federal do Rio de Janeiro) and three numerical digits.

Three mist-nets (7 m length \times 2.5 m height) were placed three or two nights a month, one hour before sundown (approximately 5:00 PM) and closed by sunrise (approximately 6:00 AM). They were positioned along the edge of the fragment, in open trails and near plants attractive to *C. perspicillata*, areas of higher capture probability of this species (CHARLES-DOMINIQUE 1991; FLEMING 1988).

Cotton bags were used to keep captured individuals before the examination. The following parameters were observed and recorded (following the methods proposed by KUNZ 1988). Species, following PINE (1972), TADDEI and VIZOTTO (1973), and CLOUTIER and THOMAS (1992). Sex. Age – individuals were allocated to age classes by examining the degree of epiphyseal ossification of the right digits I to IV (COSSON et al. 1993; KUNZ 1988). The degree of ossification was evaluated based on the transparency of the epiphysis; the most representative digit was III. The individuals with epiphyses totally ossified were regarded as adults; subadults were the ones with two bands of cartilage on at least one epiphysis; and juveniles were those whose epiphysis was totally made of cartilage. Total body mass (measured with a Pesola[®] scale – 100 g/1 g and 300 g/1 g). Length of the forearm and tibia (measured using a digital caliper). The reproductive condition was inferred by the analysis of external characters. Males were classified as either having abdominal or scrotal testis. Females as either pregnant (enlarged abdomen with a detectable foetus), lactating (enlarged nipples, and no hair around them), post-lactating (apparent hairy nipples), and non-reproductive (normal abdomen and nipples not apparent).

Data analysis

All statistical analysis followed ZAR (1996). For comparing frequency distributions, chi-square tests were used when possible, and the G test (log-likelihood ratio) was used in analyses that did not meet the assumptions of chi-square. Body mass variations across time were analysed using the Kruskal-

Wallis test, followed by the a posteriori Dunn test (paired), because the distribution of the mass data was not normal. To test the relationship between different data series, such as proportion of reproductive females and average body mass, Pearson correlation was used.

Results

During the twenty months of the study, we found four reproductive seasons in *C. perspicillata*, two with reproductive maxima and two with smaller peaks of reproductive activity. The highest peaks of reproductive females occurred during the rainy season and the smaller ones during the early dry season (Fig. 2). Proportions of reproductive adult females and reproductive adult males were positively correlated with each other ($r = 0.81$, 18 df, $p = 0.0018$). The proportion of reproductive adults varied among months in both sexes (females $G = 107.13$, 19 df; $p < 0.001$, $n = 434$; males $G = 36.84$, 19 df; $0.01 < p < 0.005$, $n = 410$).

In this study as a whole, sex ratio (M/F) for adults was 0.67, differing significantly from 1:1 ($\chi^2 = 30.17$, 1 df; $p < 0.001$, $n = 776$); females represented 60% of the total of 1,073 captures. Considering adult males and females as a whole, there was no significant variation in the sex ratio among the months studied ($\chi^2 = 23.6$, 19 df; $p = 0.16$).

Age structure did not differ for males and females in the study as a whole ($G = 6.11$, 2 df; $0.025 < p < 0.05$, $n = 932$). Pooling both sexes, there were significant differences between the proportion of age classes among months ($G = 238.04$, 38 df; $p < 0.001$) (Fig. 3). The proportion of juveniles was positively correlated with the proportion of pregnant females three months before parturition ($r = 0.92$, 17 df; $p = 0.00002$). The peaks of lactating females occurred two months after the peaks of pregnant females and one month before the peak of juveniles (Fig. 4).

The mean body mass of adults varied among months in both sexes (females, $H = 129$, 19 df; $p < 0.0001$; males $H = 37.6$, 19 df; $p = 0.0067$), and the greatest differences occurred between months of the dry season and those of the wet season (Fig. 5). Body mass varia-

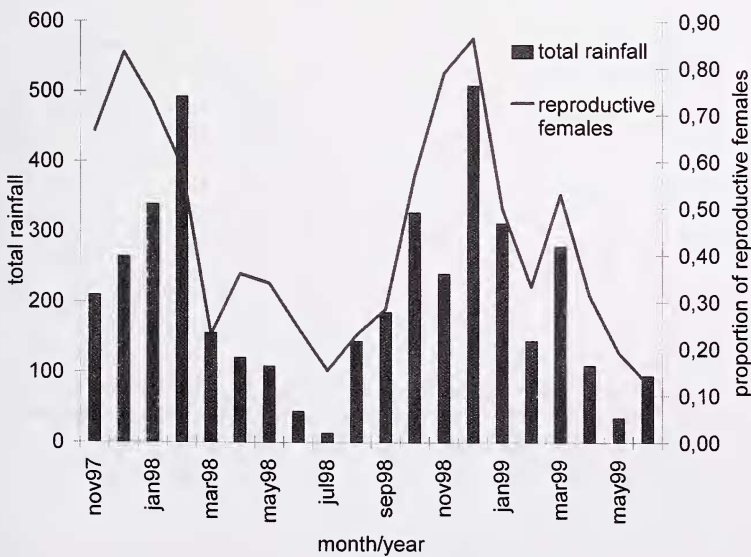


Fig. 2. Monthly rainfall and proportion of reproductive adult females of *C. perspicillata*, during the period studied.

tions in both sexes were correlated with each other ($r = 0.85$, 17 df; $p = 0.0003$). Body mass variation of adult females was positively correlated with the proportion of reproductive adult females ($r = 0.79$, 18 df; $p = 0.0034$).

Regarding activity time, the variations in the numbers of captures of adult females and adult males through the night, were correlated with each other ($r = 0.98$; 10 df,

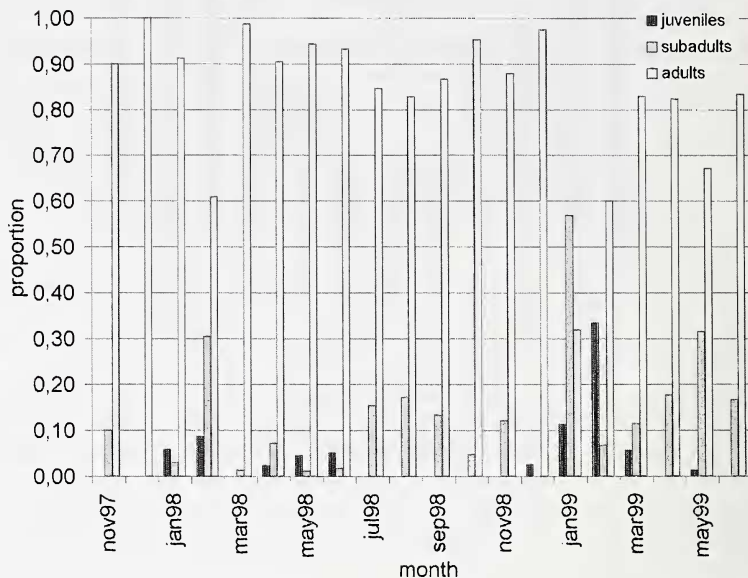


Fig. 3. Monthly variation in the age structure of the *C. perspicillata* population; values are the proportion of captures in each age class in relation to the total number of captures in each month.

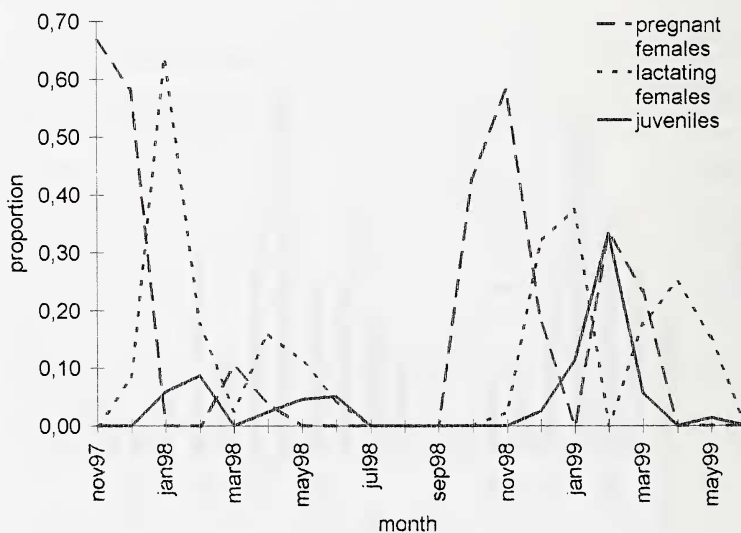


Fig. 4. Monthly variation in the frequency of pregnant and lactating adult females compared to the proportion of juveniles of *C. perspicillata*; values expressed as proportions of the total number of captures in each month.

$p = 8.0 \times 10^{-7}$) (Fig. 6). The sex ratio did not vary throughout the night ($\chi^2 = 5.57$, 11 df, $p = 0.9007$, $n = 853$). Pooling both sexes, the hourly distribution of captures differed significantly between the drier and the wetter months ($\chi^2 = 29.7$, 5 df; $p < 0.0001$, $n = 853$), as the activity was irregular during the drier months, compared to the pattern presented in the wet months (Fig. 7).

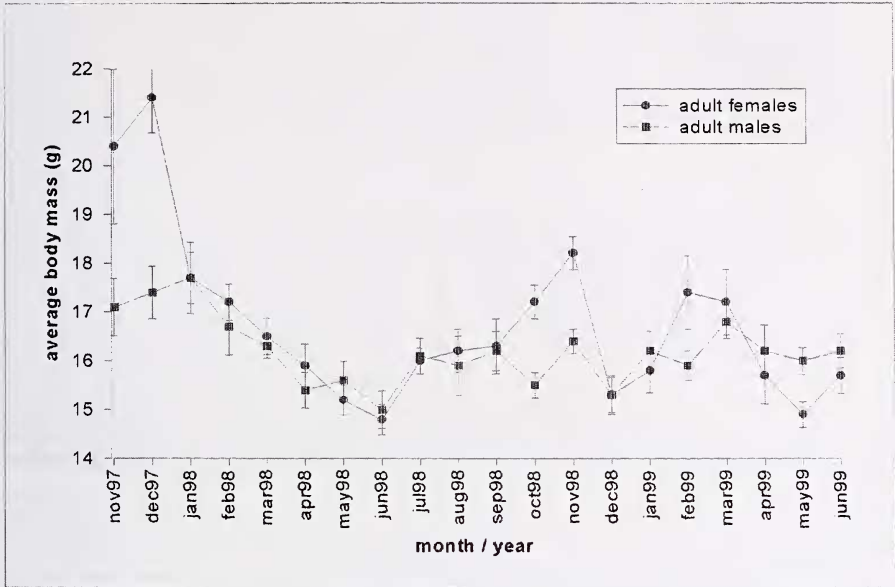


Fig. 5. Monthly variation in the average mass (g) of adult males and females of *C. perspicillata*.

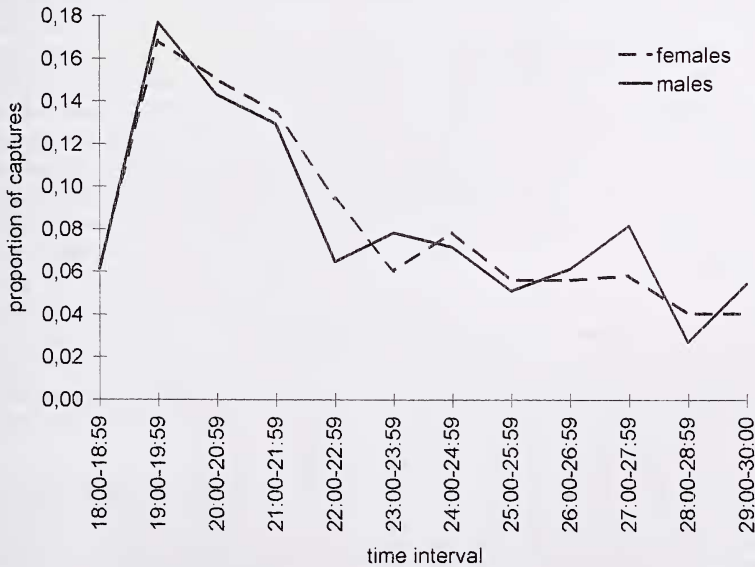


Fig. 6. Variation in the proportion of captures (related to the total) of adult males and females of *C. perspicillata* in different time intervals of the night.

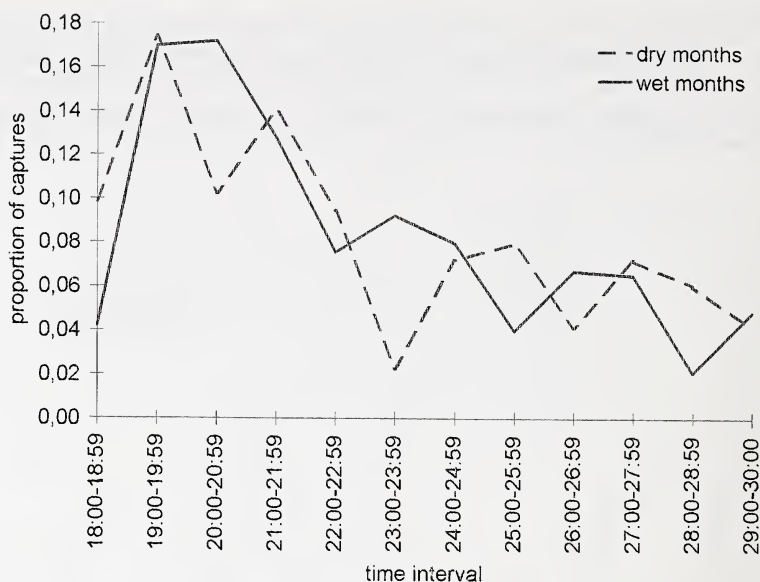


Fig. 7. Variation in the proportion of captures (related to the total) of *C. perspicillata* related in different time intervals during the night, comparing the patterns found in the wet months and in the dry months.

Discussion

The variations in the proportion of reproductive *C. perspicillata* may be best described by a pattern of bimodal seasonal polyoestry, which has already been found for this species in other studies, e.g. in Costa Rica (FLEMING 1988), French Guyana (CHARLES-DOMINIQUE 1991; COSSON and PASCAL 1994), Panamá (HANDLEY et al. 1991); and Brazil (FAZZOLARI-CORRÊA 1995). The highest reproductive peak for each year occurred during the wetter months, a time of the year where there is probably a greater availability of more nutritional food resources, specially fruits (MARINHO-FILHO 1991). During the drier months of each year, a secondary peak of reproduction occurred, probably as an effect of post-partum oestrus (CLOUTIER and THOMAS 1992). This is probably the cause of the secondary peak of reproduction a few months after the highest peak, when resources are probably in low abundance, a pattern also proposed by COSSON and PASCAL (1994). There is also a temporal relation in the reproductive activity of females and males, which could be interpreted as another evidence of post-partum oestrus. During drier months, *C. perspicillata* tends to increase the proportion of items other than fruits in its diet, especially insects, pollen and nectar (MARINHO-FILHO 1991), because fruits of its preferred understory shrubs tend to decrease in abundance. Pregnancy lasts three months on average and each female has only one youngster at a time, with very few exceptions (CLOUTIER and THOMAS 1992). This means that each female usually contributes with one or seldom two individuals a year for the population (COSSON and PASCAL 1994).

The sex ratio is reverse to what was found in studies based on samplings made close to large roosts (e.g. FLEMING 1988) or in small but very crowded roosts (e.g. COSSON and PASCAL 1994). There, males accounted for two thirds of the total number of captures. On the basis of the available data, it is not possible to know if this pattern is a consequence of a higher capture probability of females, or if there are really more females in the area. Considering that *C. perspicillata* usually forms harems, and that harem males tend to have

smaller home ranges than females, these factors combined could be responsible for the higher capture rate of females.

The direct consequence of the reproductive pattern for the total population is the change of the age structure. The major input of juveniles occurred three months after the peak of pregnancy in both the wet and the dry seasons. Compared to the age structure of other small mammals, the age distribution of this species seems to be very short at the base. Adults accounted for the majority of captures, while juveniles were less abundant. This "inverted pattern" could be explained by the demographic peculiarities of *C. perspicillata* bats: females have normally only one youngster a year, and some juveniles do not survive to reach the adult age. Besides, individuals become adult in about four months, and the mean longevity is approximately 2.5 years (FLEMING 1988). These factors can lead to a higher abundance of adults in *C. perspicillata* populations.

The variation of the body mass of adult females and males seems to be related with the reproductive seasons of *C. perspicillata*. Body mass tended to be higher during the wetter months, the same time when the ratio of females reproducing was higher. This pattern suggests that the wetter months may be the most favourable time for the species to obtain higher quality nourishment in Brazil, corroborating previous studies (e.g. COSSON and PASCAL 1994; MARINHO-FILHO 1991). Females become heavier during the highest reproductive activity, which is a consequence of pregnancy, but males also increase their body mass at the same time, corroborating the hypothesis of a difference in food abundance, as proposed in other works (e.g. COSSON and PASCAL 1994).

Following the general trend of this study, the activity (capture frequency) of *C. perspicillata* also seems to have seasonal patterns. During the wet months, the activity was more regular and concentrated, compared to the dry months, but in both cases it was higher at the beginning of the night. During the wet seasons, *C. perspicillata* concentrates its activity in the first half of the night. Probably, the availability of fruits is higher at this time of the year, and, therefore, *C. perspicillata* tends to reduce drastically its activity after obtaining enough food for their necessities. On the other hand, during the dry season, it becomes necessary to extend the period of activity, because there may be fewer fruits available in the area.

In an overview, in the Atlantic coastal forest *C. perspicillata* seems to have its ecological patterns strongly related to the climatic variations, as in other regions of the Neotropics. It seems reasonable to assume that climatic variations must be the indirect cause of the patterns, the direct cause being the variation in the availability of food, mainly understory shrubs, which is the preferred food source of the species in all the areas where it occurs. The variation in the rainfall seems to affect directly the populations of plants that this bat uses as food, and, consequently, the population of the bats.

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Zusammenfassung

Fortpflanzungsökologie der Brillenblattnasenfledermaus Carollia perspicillata (Chiroptera: Phyllostomidae) in einem Fragment des atlantischen Küstenregenwaldes in Brasilien

Das Ziel dieser Untersuchung war es, das Fortpflanzungsmuster der Brillenblattnasenfledermaus *Carollia perspicillata* (Phyllostomidae) zu erfassen und Faktoren zu bestimmen, die dieses Muster beeinflussen. Die Daten wurden über einen Zeitraum von anderthalb Jahren von November 1997 bis Juli 1999 gesammelt. Die Untersuchung wurde in Brasilien in dem Naturschutzgebiet Poço das Antas (22°30'–22°33' S, 42°15'–42°19' W) bei der Stadt Silva Jardim in der Provinz Rio de Janeiro durchgeführt. Die Datenaufnahme im Freiland erfolgte einmal pro Monat in einem 15 ha großen Waldfragment des atlantischen Küstenregenwaldes. Das Untersuchungsgebiet zeichnet sich durch eine reichhaltige Vegetation aus, die als Nahrung und zum Teil als Quartier für Fledermäuse dient. Zum Fang der Fledermäuse wurden Japanetze eingesetzt. Das Fortpflanzungsmuster von *C. perspicillata* ist durch eine jahreszeitliche Rhythmik bestimmt mit einem Maximum in den Regenmonaten (September bis Mai) und einem schwächeren Maximum in den Trockenmonaten (Juni–August). Drei Monate nachdem die meisten Weibchen trächtig waren, kam das Maximum an juvenilen Tieren. Die durchschnittliche Körpermasse der Weibchen und die Aktivitätsrhythmik von *C. perspicillata* veränderte sich von den Regen- zu den Trockenmonaten. Während der Regenmonate trat nur ein sehr ausgeprägtes Aktivitätsmaximum pro Nacht auf. Während der Trockenmonate war die Aktivität gleichmäßig über die Nacht verteilt und es trat kein ausgeprägtes Maximum auf. Diese Muster deuten bei *C. perspicillata* eine Beziehung an zwischen Fortpflanzungsrhythmik und Regen. Die Regenmenge kann die Verfügbarkeit der Nahrungsquellen beeinflussen und folglich auch die Aktivität der Fledermäuse.

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